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Art. III.—*The Biology of the Silverfish,* Ctenolepisma longicaudata *Esch. with Particular Reference to its Feeding Habits.*

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Contents.

I. Introduction.

Ctenolepisma longicaudata was first described by Escherich in 1905 from material collected in South Africa. It has, since been found in Palestine, Seychelles, and the New Hebrides, and the first record from Australia was made by Silvestri in 1908 from material of the 1905 Hamburg expedition. It is widely distributed in Australia and collections have been received from all the coastal regions, as far north as Cairns, and as far inland

as Broken Hill. During the last fifteen to twenty years it has become a household pest of economic importance, and in 1935 investigations into its control were undertaken by the Commonwealth Council for Scientific and Industrial Research. The work carried out at the School of Agriculture of the Melbourne University started as an inquiry into the attack upon wallpapers; but the control measures which were evolved necessitated the study of the insect's biology with particular reference to the reasons for its food preferences, and the extent to which it is affected by climatic conditions.

II. Experimental Methods.

Silverfish have a long life cycle. They reach sexual maturity in two to three years, and continue to grow for about five years longer, moulting three to five times each year. As it was necessary to use adults for the feeding tests, insects were collected in various buildings, mainly at night, and stocks of these were held in lots of one hundred in 200 cc. glass beakers, and were fed on tissue paper, gummed paper, artificial silk, and ground whole wheat and yeast. The beakers were kept in a cupboard in which a high humidity was maintained by open tubes of water, since previous tests had shown that in dry conditions, as, for example, in open containers on the bench, the insects died within one month. These conditions proved satisfactory for reproduction and growth. Cotton-wool was provided as a nidus for egg laying and facilitated the collection and removal of the eggs. Nymphs were reared on the same food as the adults.

In the tests on the food preferences the materials to be compared were subjected to the attack of twenty to forty silverfish held in a Petri dish containing two pieces of each material. As soon as the attack showed, the edible materials were removed, so that the silverfish were confined on the remaining pieces under semi-starvation conditions. In this way, any variation in the feeding stage of the various individuals was eliminated, and the tests were sufficiently rigorous to ensure that the materials would be attacked if at all edible. The pieces were folded so that the insects had easy access to all the materials. The whole series was duplicated. All were held in closed tins with tubes of water and kept at 24°C. for the two to three months of the test.

In the tests on wallpapers, the insects were confined on the surface of the sample by pushing the piece to the bottom of a 1-inch glass vial. Three silverfish were used on each sample. The tests were duplicated and the results were confirmed by subjecting selected samples pasted on glass to the attack of eighty silverfish. A section of these samples is shown in pl. II, fig. 2.

III. Feeding Habits.

Observations during the past three years have shown that silverfish, even the 2nd instar nymphs, range far in search of food, and include both animal and plant remains in their diet, as well as materials of economic importance such as paper and artificial silk. They are easily disturbed and are seldom observed eating; but at various times, they have been found indoors feeding on a variety of materials including bread crumbs, a dead moth, a piece of dried grass, and a fragment of the thorax of a beetle in which the muscles were still fresh.

1. Crop Contents.

Further information about the nature of the substances which are included in the normal diet, was obtained from an examination of the crop contents of more than sixty insects which were collected in various buildings.

The origin of the large fragments could be determined from their structure, and some of the stages of decomposition were identified by comparison with the crop contents of silverfish which had been given a diet of grass, paper, wool, cotton or artificial silk. The staining reaction of the fragments was tested with Iodine, Sudan III, Phloroglucin and Hydrochloric acid, Herzeberg's stain, and Lieberman's reagent. Herzeberg's stain was particularly useful for showing the presence of cellulose derivatives even after the structure of the plant cells had been completely destroyed.

Usually the crop contained material from one source only. Evidently the silverfish made a large meal from any edible material which it discovered. Insects collected indoors had frequently been feeding on plant tissue a short time previously. Many fragments found in the crops were so large that the epidermis and the cortical and vascular tissue could still be distinguished (pl. II, fig. 1B). The epidermis with stomata and hairs, and the vascular tissue with thickened and pitted walls were easily recognized. In many cases the cells still contained chloroplastids, and even after these had been broken down, the green colour of the chlorophyll persisted in the crop for some time. Many other groups of cells with various kinds of thickening could not be identified.

The fragments in many crops resembled those found among plant debris. Sand grains and pollen grains (pl. II, fig. 1A), Protococcus in both active and resting stages, and fungal spores and hyphae could be recognized (pl. II, fig. 1C). In some cases the hyphae were still living, and in one case the spores of *Ustilago hordei* were identified.

Four of the crops examined were almost completely filled with starch grains. One of these insects had been collected from a decaying tree, but the source of the starch could not be located.

Insect remains form part of the diet, and frequently setae, pieces of chitin (pl. II, figs. 1D and F), scales and tracheae were found in the crop. Animal hairs were found in only two of the crops.

In view of the varied nature of the crop contents it was interesting to see to what extent the dust of the room was a potential source of food. The dust was collected with a vacuum cleaner from behind the skirting boards and window frames of two lecture rooms. On examination the following materials were found; crumbs, small cellulose fibres, both single and in masses, woody fragments, insect legs, feelers, and claws, fragments of leaves and dried grass, string and sawdust. Even dust, it would seem, provides a varied diet for the insects.

2. Range of Materials Attacked.

To find the range of substances the silverfish would eat, various materials were subjected to the attack of groups of five insects for two months, no food other than the material under investigation being provided.

Artificial silk and cotton fabrics were readily eaten. Wool fabrics were generally not damaged, although occasionally a few fibres were found in the crop. Wool felt, flannel, carpet, fur felt, and natural silk were not damaged.

Attack on materials which were otherwise unpalatable, could be encouraged by smearing them with a palatable mixture of sweetened flour paste. In the course of the removal of this layer some of the fibres of the material were eaten, and occasionally the attack extended deep enough to damage the fabric. The unpalatable material, e.g., wool, silk, or sawdust was slowly digested. In the crop the fibres of wool were broken transversely into short lengths, the epidermal sheath flaked off, and the cortical cells frayed at the ends of the fragments. The cortical cells were apparently digested, for few were found in the hind intestine, though short lengths of the undigested fibres were sometimes found there.

3. Food Requirements of Adults and Nymphs.

Although the silverfish is normally an active feeder it can survive long periods without food. An experiment was made with twenty adult insects in separate containers (1-inch glass tubes). The first died after 21 days, and the others followed at intervals, the last three living 252, 276, and 307 days respectively.

A diet of cellulose alone was sufficient to support a longer life. The death rates of twenty adults fed only with filter paper were noted and in this case the last three insects lived 449, 576, and 636 days respectively.

A more adequate diet is necessary for the nymphs. Four groups each of twenty newly hatched nymphs were kept on various diets. The first group was given no food and eighteen survived the first ecdysis, but died early in the second stadium. The second group was given paper and flour. Eighteen of these insects survived the second ecdysis but died during the third stadium. The remaining two in both groups ate the dead bodies and cast skins of the others, and survived to the fifth instar. The third group was given paper, flour and casein. Most of them survived until the fourth and fifth instars, and only one of the dead bodies was eaten. The fourth group was given ground wheat and yeast in addition. Apparently this made an adequate diet, for on this the nymphs have been reared for eighteen months.

On the inadequate diets the food reserves were depleted by metabolism and ecdysis. The fat content of adults starved, or fed with cellulose, was reduced from 20 per cent. to 7 per cent. Normal silverfish contain 9 per cent. nitrogen. The cast skins, which weigh 5 per cent. of the dry weight of the body, contain 6 per cent. fat and 11 per cent. nitrogen, so that, with each cast skin 1 per cent. of the fat and 6 per cent. of the nitrogen of the body is lost. (These analyses were very kindly carried out by Mr. G. Ampt, of the Chemistry Department of the Melbourne University.)

4. Taste.

Silverfish are sensitive to the taste of certain substances even when these form only a small part of a mixture. Their behaviour suggests that the labial palps are the organs most sensitive to taste, the sense being probably located in the small papillae which occur on both sides of the tip (fig. 1c).

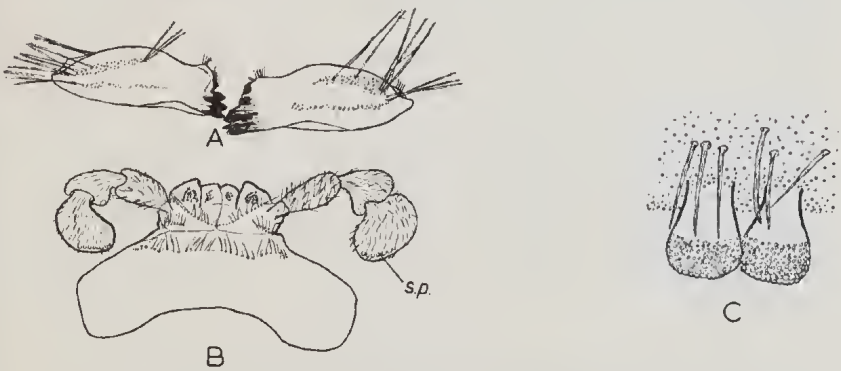

Fig. 1.—*A*. Mandibles. *B*. Labium × 14. *C*. Sensory papillae of labial palp × 300. *s.p.* sensory papillae.

The action of the mouth appendages during feeding was watched on silverfish confined in an optical cell $3\frac{1}{2}$ inches square and $\frac{1}{2}$ inch deep. The ventral side of the head was observed by means of a tilted mirror. Small heaps of powdered materials,

viz., flour, ground sugar, casein, fine chalk, and crystallized sugar were placed about $\frac{1}{4}$ inch from the edge. As the silverfish under observation moved about, it came into contact with the powder. This was touched first by the antennae, then by the maxillary palps, and then by the labial palps. The antennae and maxillary palps seemed to behave in the same way towards all the powders; but the labial palps immediately "scooped" the palatable powder, ground sugar, towards the mouth. The other powders were frequently touched by the labial palps, but the flour and casein were only occasionally pushed into the mouth. No attempt was made to eat the chalk or the crystallized sugar. The grains of the latter were probably too large.

The scooping action of the labial palps is characteristic; the expanded terminal segments act as "shovels" and push the material towards the maxillae (fig. 1B).

The labial palps are able to detect the palatability of the material before it is eaten. This sensitivity may be assisted by fluid from the mouth, for on some of the wallpaper mixtures (see below) there was a "water mark" of concentrated colour around the teeth marks and on certain parts of the undamaged surface. The "water mark" showed only on mixtures containing dextrin, and tests with droplets of water showed that only in these mixtures is the pigment held in such a way that a water mark will remain.

On a hard surface such as that of wallpaper, the mandibles (fig. 1A) are worked with a scraping movement. The mandible on the left side, which lies ventral to that on the right side, takes a wide sweep and scrapes towards the centre. These scrapings are then gathered by the right mandible, and, together with the small amount it accumulates itself, are pushed into the mouth. The scraping marks of the teeth can be clearly seen at the edge of the damaged parts (pl. I, fig. 2).

On a fibrous surface such as that of textiles and paper, the laciniae tease and lift the material towards the mandibles which chew through the connecting strands (pl. I, figs. 3 and 4). The pieces of fabric removed in this way are sometimes so large that the mesh can still be seen on the fragments in the crop.

Owing to this sensitive taste different kinds of such goods as wallpaper, writing paper, and artificial silk are attacked to different extents.

Wallpaper:—The effect of the different ingredients in wallpaper was tested on more than 9,000 sample mixtures.

The palatable materials in wallpaper are the various sizes mixed with the pigment and filler. The sizes used are starch, dextrin, casein, gum and glue. Only the mixtures containing starch and dextrin were extensively attacked, the colour being removed from the surface of the paper before the paper itself

was eaten (pl. II, figs. 2 and 3). The mixtures containing casein were eaten to a small extent, and as the insects did not continue feeding around the areas first attacked, only small areas of colour were removed. The mixtures containing gum and glue were not attacked unless the paper beneath was exposed at a scratch, and then the colour was removed as the paper was eaten.

All the sizes, even the apparently unpalatable gums and glues, were readily eaten when dissolved and dried into a thin layer on the surface of paper, so it is rather difficult to understand why the colour mixtures containing gum and glue proved so unpalatable.

Black, yellow, red and blue mixtures were tested, but the nature of the pigment had little effect on the extent of attack, except, perhaps, that it was rather slower on the black and yellow mixtures. The addition of filler lowered the percentage of size in the mixture and decreased the palatability.

It was interesting to watch the behaviour of a silverfish presented with pieces of both palatable and unpalatable wallpaper. The insect was held in a petri dish, and during its wanderings it walked over the surface of the unpalatable wallpaper several times. Then it touched the palatable wallpaper and immediately started to feed continuing for three hours, with only eight pauses of one to two minutes each. During the next hour it moved about the dish, walking over both the papers. Every time it walked over the palatable colour it took a few bites, but only twice did its jaws move when it was in contact with the unpalatable wallpaper, and even then no marks were made on the surface.

The paste used for fixing the papers to the walls was readily eaten when exposed at joins, but did not influence the attack on the surface. It had been thought at the outset of the investigation, that this paste attracted the silverfish to the wallpaper.

Writing, Printing and Wrapping Papers:—It was frequently noticed that only some of the sheets in a pile of papers suffered extensive damage; but that subsequently, all were readily eaten when the silverfish were confined on the papers. This localized attack could not be attributed to the position, for adjacent pieces of similar paper were attacked to different extents. Rather, it seemed that once the silverfish had made an attack, they tended to continue feeding there, with the result that the damage was concentrated in a few particular places.

The extent of attack was determined also by the nature of the paper. A wide range of papers, paper boards and paper pulps was tested. Mechanical pulp was not attacked, Kraft and Esparto pulps were slightly attacked, but bleached and unbleached sulphite pulps were readily eaten. A consideration of the nature of the pulps in the tested papers showed that all the papers which were readily eaten consisted of 100 per cent. chemical pulp, the

degree of attack depending on the finish and fillers used. The papers only slightly attacked, including "writing" paper, newsprint, and other printing papers, contained mechanical as well as chemical pulp.

This unpalatability of the mechanical pulp influenced the attack on the surface of wallpaper. The papers used in the tests contained 100 per cent., 52 per cent. and 45 per cent. chemical pulp respectively. The rubbings on the paper containing 100 per cent. chemical pulp showed more extensive damage than those on the other two papers. Large areas of colour were completely removed as the paper beneath was eaten. On the other two papers small bites were distributed over the surface of the colour, and were more extensive on the paper containing the greater amount of chemical pulp.

It seemed remarkable that this small difference in the amount of mechanical pulp in the paper should have such an effect on the attack on the surface, and further tests were made on papers containing mechanical pulp. These were obtained through the courtesy of the Forest Products Division of the Commonwealth Council for Scientific and Industrial Research and the Australian Paper Manufacturers and comprise:—

(A) 100 per cent. bleached sulphite pulp.
(B) 100 per cent. chemical pulp from Eucalyptus wood.
(C) 80 per cent. bleached sulphite—20 per cent. mechanical (6 per cent. clay and rosin).
(D) 75 per cent. unbleached sulphite—25 per cent. mechanical.
(E) 52 per cent. sulphite—48 per cent. mechanical. (6.4 per cent. ash.)
(F) 45 per cent. sulphite—55 per cent. mechanical. (11.4 per cent. ash.)
(G) 30 per cent. sulphite—70 per cent. mechanical. (Newsprint.)

The papers were dipped in methylene blue so that any slight surface attack could be detected as the more deeply stained fibres on the surface were removed. Comparison with uncoloured samples showed that the methylene blue did not affect the attack. During the first ten days, papers A and B containing 100 per cent. chemical pulp were readily eaten, and after 30 days papers C and D containing 20 and 25 per cent. mechanical pulp showed some attack; but the papers with more than 48 per cent. mechanical pulp were not attacked even after 90 days. In each case the papers were removed from the test as soon as the attack was seen.

As mentioned above, it had been noticed that the composition of the paper affected the extent of attack on the surface coating. This observation was confirmed by coating the papers A to G

with a palatable gum which was dyed crimson to facilitate observations. The gum was readily eaten off the papers of chemical pulp and the attack extended to the paper. But the gum on the papers of mechanical pulp was much less eaten, and even after 90 days very little attack occurred on the gum coating on paper F and the newsprint.

As no commercial papers containing between 25 per cent. and 45 per cent. mechanical pulp were available, sample papers were made from weighed quantities of mechanical and bleached sulphite pulp and the final composition of the papers was checked by counting the fibres under the microscope using the method described by Gaff, 1935. The papers thus prepared contained 64, 33, 30, and 23 per cent. mechanical pulp. Of these, the paper with 23 per cent. mechanical pulp was well eaten, the papers with 30 and 33 per cent. were slightly eaten, but no attack was made on the papers with 64 per cent. mechanical pulp even after four months.

It was concluded from these experiments that:—

1. Papers containing 100 per cent. chemical pulp—sulphite, bleached and unbleached—are readily eaten.
2. The presence of even 20 per cent. mechanical pulp greatly reduces the attack.
3. Papers containing 45 per cent. or more mechanical pulp are not damaged.

The Cause of the Unpalatability of Mechanical Pulp:—An attempt was made to find the cause of the unpalatability of the mechanical pulp. In the preparation of mechanical pulp, the wood, mainly spruce and hemlock, is rubbed into small fragments. In the preparation of chemical pulp the substances which impregnate the walls of the wood fibres are removed, and the cellulose itself is partly decomposed. Thus the fibres of the chemical pulp are different from those of the mechanical pulp, both in chemical composition and physical texture, and probably both these factors contribute in determining the palatability of the pulp. In the Kraft process the chemical action is not carried so far, and some of the unpalatable properties of the mechanical pulp still remain.

Very little is known about the chemical nature of the materials which impregnate the cellulose walls of a wood fibre, but various materials have been isolated from the mechanical pulp extracts, and an attempt was made to find the effect of these materials on the palatability of the pulp.

First the mechanical pulp was extracted successively with ether, alcohol, hot water and 5 per cent. sodium hydroxide. Other samples of the pulp were extracted separately with the above solvents and 3 per cent. sulphuric acid. "Bond" paper was soaked in these extracts for 24 hours and then subjected

to the attack of silverfish. It was found that all the papers were readily eaten except those impregnated with the ether extract, which delayed the attack for three months. The materials extracted were decomposed by exposing the impregnated paper to sunlight for two weeks. The extract was bright yellow. It could be decolourized by charcoal or barium sulphate, but the colourless extract did not render the paper unpalatable.

The effects of various chemicals associated with the resins and fats of wood were also tested by impregnating the Bond paper with solutions of the substances in carbon tetrachloride. Oleic and linoleic acids proved ineffective, but abietic acid prevented attack for one month. Samples of wood extracts, lariciresinol, sitosterol, matairesinol, and a benzene-alcohol extract of paper pulp resin were kindly supplied by Dr. R. D. Haworth of the University of Newcastle-on-Tyne. Three per cent. solutions in acetone were used. Both lariciresinol and matairesinol prevented the attack on paper; but both caused the paper to turn a light brown, and both made it slightly sticky.

It was thought that the physical texture of the mechanical pulp might contribute to its unpalatability, and an attempt was made to test this by preparing papers from the mechanical pulp after it had been extracted with water, acid, alcohol and ether, as in the above tests. Some difficulty was experienced in making paper from the mechanical pulp because it would not hold together, and it was hard to see if any attack occurred on the surface. Certainly the attack, if any, was very slight.

The state of the cellulose itself also affected the palatability of the paper. Spruce wood pulp is high in hemicelluloses which are readily degraded during the chemical pulping. Further, as prepared for the "Bond" paper, the pulp has a large percentage of fragmental fibres produced during the beating, and both factors probably contribute to the palatability of this type of paper. In contrast to this, the pulp for filter paper (which is not readily eaten) is prepared from rag cellulose low in hemicelluloses, and so treated that all the degraded celluloses are removed leaving only the resistant α-cellulose. Duplicating paper (d.c. 48, from Thomas Tait) which also is not readily eaten contains a high percentage of Esparto fibres. These fibres are low in hemicelluloses, and, since they are only lightly lignified the treatment is so mild that little degraded cellulose is produced. The pulp is beaten for only a short time. It would seem therefore that this pulp, too, is not easily digestible.

Even though the silverfish will eat and digest any kind of cellulose, particularly if it is made palatable by mixing, for example, starch paste with sawdust, or large amounts of chemical pulp with the mechanical pulp, it is understandable that the attack should be more pronounced on the celluloses which are the most easily digestible.

Deterrent Sprays:—Since it is not possible in practice to eliminate the attractive materials from the wallpaper, an attempt was made to find some deterrent which could be sprayed on the surface. The 69 substances selected for the tests were derivatives of phenol, cresol, and salicylic acid, and salts of barium, mercury, tin and antimony (see Appendix). Water, methylated spirits, and a petroleum fraction "White Spirits" were used as solvents with several concentrations of each substance. The protection to both wallpaper and "Bond" paper was tested.

The appearance of the attack on some of the wallpapers suggested that areas were left uncovered as the spray dried. The distribution of the spray was tested by the reaction of ferric chloride on papers sprayed with salicylic acid, and by spraying with methylene blue. It seemed that the spray covered the surface, but did not penetrate far, so that underlying unimpregnated colour and paper fibres were readily exposed. An attempt was made to reduce the surface tension of the alcohol and water solutions by the addition of cetyl alcohol, but the deterrent action of the sprays made in this way did not last longer than before.

Finally a 1 per cent. solution of tricresylphosphate in White Spirits, and a half saturated solution of Tartar emetic in water were selected. Both protected the surface for nine months. A small amount of damage occurred on the Tartar emetic sprayed paper, but the insects died. The insects made no attempt to eat the paper sprayed with tricresylphosphate. Apparently they detected its unpalatability without biting the surface.

Adhesives:—Twenty-four commercial adhesives were tested in thin layers spread on "Bond" paper. The pastes, gums, dextrin, casein, and cellulose adhesives were all readily eaten off the surface of the paper. The glues were less readily eaten, the attack occurring only on the edges. Only two adhesives, a gum and a glue, were not attacked, and it is probable that the preservative in these acted as the deterrent.

Tricresylphosphate and Tartar emetic were added to a starch paste and a gum. Attack on the paste was prevented by 4 per cent. of the tricresylphosphate, and 5 per cent. of the tartar emetic (both per cent. weight of flour). Attack on the gum was prevented by 1 per cent. Tartar emetic and 2.5 per cent. tricresylphosphate (by weight). With lower concentrations of the deterrents the paper was eaten, and at still lower concentrations the adhesive itself was eaten off the surface of the paper.

Artificial Silk:—Artificial silk is very readily eaten (pl. I, figs. 3 and 4), but treatment with certain materials for fire proofing and water proofing rendered the silk so unpalatable that it was eaten only by starved insects. When this treated silk was smeared with a palatable mixture of sweetened flour paste, the paste and the silk underneath were readily eaten, and the

attack extended to the surrounding strands. The tricresylphosphate spray rendered the untreated silk so unpalatable that, when soiled in the same way, the paste was eaten from between the strands of the material with very little damage to the strands themselves.

Poison Baits:—The taste sensitivity of the silverfish was important also in the preparation of poison baits. These baits were developed by the Division of Economic Entomology of the Commonwealth Council for Scientific and Industrial Research (Jr. C.S.I.R., 1939, p. 85).

5. Digestion and Absorption.

The Process of Digestion:—The digestive tract is simple (fig. 2). The large thin-walled crop extends to the third abdominal segment—more than half the length of the body. A pair of large salivary glands which lie around the anterior end of the crop, open on the hypopharynx, and may be the source of the small amount of fluid which moistens the food during chewing. The food is moved about slowly in the crop (peristalsis is not strong) and is further broken down by the teeth of the gizzard. It would seem that some chemical decomposition also takes place in the crop as the material which passes into the mid-intestine is very finely divided. There is no evidence that any secretion occurs in the crop and, possibly, digestive fluids pass forward from the mid-intestine.

The semi-fluid mass passes from the gizzard into the mid-intestine. In the anterior region of the mid-intestine, the material lies in the sacculi, but in the posterior region it is held within a well-marked peritrophic membrane. Presumably this membrane is secreted by all the cells of the mid-intestine, for no special secreting cells and "press" (Wigglesworth, 1929), could be seen in the stained sections.

The hind intestine is lengthened by an anterior, dorsal, loop before it joins the rectum. The epithelium of the hind intestine is deeply folded, and the walls of the rectum are thrown into six well-marked longitudinal folds, and two rows of papillae surround the anus. This increased surface of the proctodeum is presumably concerned with the extraction of water from the faeces which are nearly dry when extruded.

The rate of digestion of paper was observed. A starved insect was given access to the paper for two hours. Within twelve hours some of the paper had passed into the mid-intestine, and an examination after 48 hours showed that all the fibres in the crop had been completely destroyed. Residual material first appeared in the hind intestine 24 hours after feeding and faeces were passed until the fifth day. With more indigestible material, e.g., insect remains and wool, faecal pellets continued to be expelled at intervals for seventeen days.

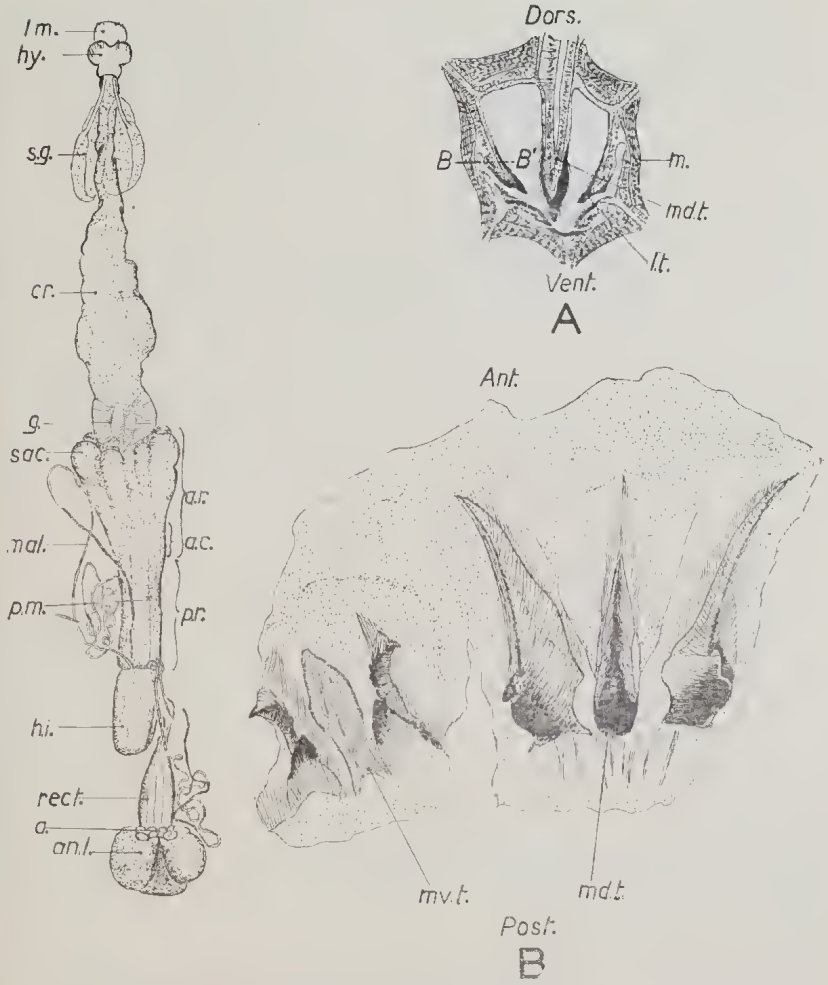

FIG. 2.—Alimentary canal and crop; *A*, Transverse section of crop and *B*, Crop opened on one side B-B¹; *a.* anus; *an.l.* anal lobes; *cr.* crop; *g.* gizzard; *hy.* hypopharynx; *h.i.* hind intestine; *lm.* labrum; *l.t.* lateral tooth; *m.* muscle; *md.t.* mid dorsal tooth; and *mv.t.* mid ventral tooth of gizzard; *mal.* malpighian tubule; *a.r.* anterior region; *p.r.* posterior region and *a.c.* absorbing cells of mid intestine; *p.m.* peritrophic membrane; *rect.* rectum; *sac.* sacculi; *s.g.* salivary glands.

Cellulose Digesting Bacteria:—Insects feeding on cellulose usually depend on the lower organisms in their intestine to assist in the digestion of the cellulose, and it was found that cellulose digesting bacteria could be readily cultivated from the contents of the crops of silverfish.

Thirty ccs. of Winogradsky's medium (1929), after sterilization, were mixed with the expressed contents of one crop. A piece of filter paper was half immersed in the liquid, and kept at 24°C. for one week. The paper at the water level became

brownish, and below the water very gelatinous. When examined under the microscope the fibres had the "chewed" appearance typical of the action of these bacteria. There were many cocci and bacilli both on the surface and inside the fibre. The paper in the uninoculated salt medium was unchanged.

Fungal hyphae, which were frequently found growing in the crop also may aid in digestion.

The pH of the Alimentary Canal:—An attempt was made to measure the pH of the contents and cells of the alimentary canal by feeding the silverfish on paper dyed with indicators. Although conditions were not suitable for determining the depth of colour of the indicator, the change in colour could be seen, and, by using a range of indicators, the pH of the region determined. The indicators used were:—2, 4 dinitrophenol, phenol red, naphtholphthalein, tropoeolin 000, cresol red, brom-thymol-blue, brom-cresol-green, methyl red, para-nitrophenol, brom-cresol-purple, meta-nitrophenol, and thymol blue. The colour of the indicator was noted in a rapidly dissected insect. There was no disagreement in the results from any of the indicators.

The pH of the crop was always the same as that of the food. The pH of the anterior region of the mid-intestine was difficult to see, owing to the thick walls, the fluid nature of the contents, and the rapid entrance of food from the crop. It appeared to be between 4.8 and 5.4. The pH of the posterior region of the mid-intestine was between 6.4 and 7.0. The pH of the hind intestine was lower, between 2.6 and 3.8, possibly owing to acid excretory products.

Several of the indicators, viz., meta-nitrophenol, para-nitro-naphtholphthalein, tropoeolin 000, cresol red, and brom-cresol-green, were absorbed in the cells of the anterior part of the mid-intestine in apparently the acid form, but they no longer responded to pH changes.

Several of the indicators, viz., meta-nitrophenol, para-nitro-phenol and methyl red, were found to be unsuitable because they were changed in the intestine and no longer indicated pH, or because their colour change was indefinite under these conditions.

The indicators were fed to the silverfish also on casein and sugar, and it was found that the nature of these foods did not affect the pH of the alimentary canal.

Redox Potential:—Using the same methods as above, the indicators, o-chlorophenol–indophenol, toluylene blue and methylene blue were fed to the insects.

Ortho-chlorophenol-indophenol was decolourized in all parts of the alimentary canal. Toluylene blue was present in the oxidized form in the crop and mid-intestine, where it could still be decolourized by sodium sulphite. Methylene blue was present throughout the alimentary canal in the oxidized form.

The Distribution of Certain Dyes:—These indicators and other dyes stained other parts of the body as well as the mid-intestine. When absorbed in these tissues the methylene blue could still be decolourized with hot sodium sulphite, but the toluylene blue could not be decolourized and no conclusions could be drawn about the Redox potential of these parts.

The methylene blue was absorbed by the mid-intestine, appearing in the cells of the anterior region within 24 hours, and in those of the posterior region on the fifth day. In each case the cells appeared to be filled with blue globules which were larger in the anterior region than in the posterior region of the mid-intestine. The crystals of excretory material in the faeces stained blue, and within four days the methylene blue appeared in the malpighian tubules located in indefinite patches of cells along their length. By the twelfth day the methylene blue coloured the immature eggs, the yellow cells of the ovarioles, and the edges of the fat bodies.

Sudan III was fed to the insects on ground wheat. Part was readily absorbed by the cells of the mid-intestine. Three days after feeding, red globules appeared in the cells of the malpighian tubules; the fat bodies were coloured a deep pink; the immature eggs, and the material inside the dilated portion of the vasa differentia were coloured pink; the accessory glands of the female were coloured red. In one female the eggs had passed into the calyx. The contents were coloured pink, but it is not known whether the dye penetrated the chorion, or whether the egg stained before this had formed. The colour persisted in the ovarioles for about twenty days, and even after 85 days the cells of the mid-intestine and the fluid in the crop still remained red, though, by this time, none of the other organs retained any Sudan III.

The appearance of the dyes absorbed in the mid-intestine was different in the cells of the posterior half from those in the anterior half. Two more regions in the anterior half (fig. 2) were distinguished by the appearance of the absorbed toluylene blue and Sudan III. These latter differences could not be correlated with any structural differences in the sections stained with Heidenhain's haematoxylin, and their particular function in digestion is not known.

A number of other red dyes were also tested in order that the form of the alimentary canal could be photographed through the semi-transparent chitin of the nymph. Magenta, carmine, and aniline red were all readily eaten, but were not absorbed in the mid-intestine, being merely concentrated in the faeces. Eosin and orange G. proved toxic.

IV. The Life History.

The first observations on the life history of the silverfish were made by J. W. Raff in 1933. The life cycle extends over several years. The nymphs develop with very little change in form. Sexual maturity is reached in $2\frac{1}{2}$ to 3 years and the adults continue to grow, moult, and lay eggs for at least three years longer.

1. The Egg.

Eggs are laid in lots of from two to twenty. In normal conditions they are pushed by the long ovipositor about 2 mm. into a crevice and so are rarely seen. Some have been found under the edge of a piece of pasted paper, and in a crack in a wooden drawer. They are oval and measure 1.15 × 0.83 mm. (average of 15). When first laid they are cream coloured and smooth, but after three days the chorion darkens to a yellow and shows shallow reticulated markings.

The young insect bursts the shell with a small ridge on the frons, the hatching organ (fig. 3). This is shed with the first exuviae. The crop pulsates vigorously during hatching. It is filled with air, although the mouth appears to be closed throughout the first instar. After about five minutes the insect wriggles

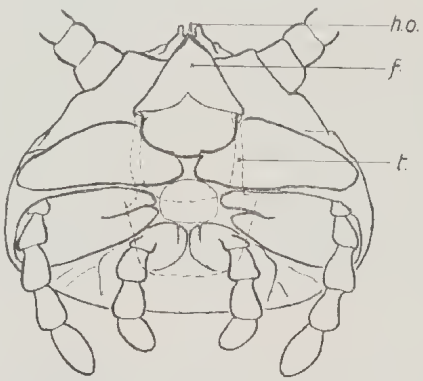

Fig. 3.—Head of 1st instar from ventral surface showing hatching organ and tentorium; *f.* frons; *h.o.* hatching organ; *t.* anterior arm of tentorium.

free of the shell. In captivity almost all of the eggs hatched, and there were very few deaths during the early instars. Other references to the hatching organs of *Lepisma saccharina* are included in the Bibliography (Heymons, van Emden, Wigglesworth).

2. The Early Instars.

The development of the first fourteen instars was followed. The length of the successive stadia showed considerable variation even at a constant temperature of 23°C. (Table I.). The distinctive characteristics of the successive instars were not easy to

define, for these resembled each other closely in all but the few features described later. The new instars were distinguished by their complete coat of scales which are tightly adherent during the first few days of the stadium. In general, growth results in a gradual increase in size, and in the elaboration of both the internal and the external structures present in the young insects. The feeding habits are the same. The cells of the mid-intestine are already differentiated as in the adult. The gizzard has the same form as in the adult though there are fewer serrations and hairs on the teeth. The malpighian tubules are relatively large until about the twelfth instar. The eyes have twelve ocelli as in the adult, but these are rather more rounded.

Table I.—Duration of Early Stadia at 23°C.

Instar.	Number of Insects.	Average Length of Stadia Days.	Range Days.	Instar.	Number of Insects.	Average Length of Stadia Days.	Range Days.
1	40	3	3 4	8	16	37	24–46
2	14	11	6–15	9	17	41	25–64
3	20	13	10–15	10	9	39	27–57
4	4	17	16–19	11	6	39	24–51
5	10	23	16–35	12	2	39	33–46
6	16	25	16–37	13	2	43	40–47
7	18	31	19 46				

As the silverfish is not heavily chitinized, and the segments are easily stretched, measurements of the total length of the body were of little value. Instead, the measurement of certain organs which have well defined limits, and which do not change during the stadium, were compared. The following organs were selected (fig. 4) :—

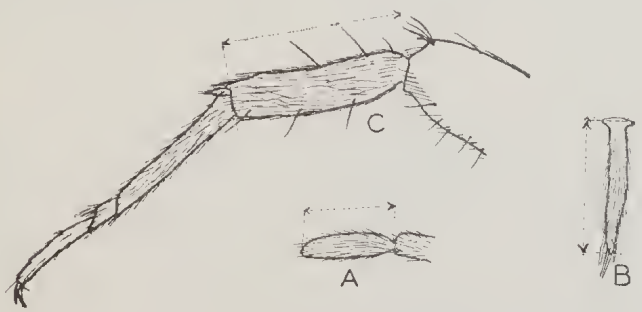

Fig. 4.—Parts used for comparative measurements of the early instars; *A*. Terminal segment of maxillary palp; *B*. Style; *C*. Anterior edge of metathoracic leg.

(*a*) The terminal segment of the maxillary palp.

(*b*) Styles.

(*c*) The anterior edge of the tibia of the metathoracic leg.

The antennae and posterior appendages were also measured when these were complete.

One hundred insects were used. They were kept at 23°C. and five to ten individuals of each instar were killed and mounted in De Faure's fluid so that the measurements could be made.

Preliminary observations on the change in size of the selected organs during the stadium showed that no further change occurred after the second day. (The measurements were usually made about four days after ecdysis.) Since it was necessary to kill the insects to make the measurements, the increase in size of an individual could not be determined. The organs of both the right and left side were measured and these were found to be usually the same size. (Exp. error ± 0.003 mm.) When the measurements differed, the mean of the two was used. The individuals of any one instar varied considerably, but a consideration of all the information enabled the instar to be decided with some degree of certainty. The average measurements for each instar are shown in Table II. The lengths of the styles

TABLE II.—AVERAGE MEASUREMENTS (MM.) FOR THE INSTARS 1–14.

Instar.	Anterior edge of head to posterior tip of abdomen.	Terminal Segment Maxillary palp.	Anterior Edge Metathoracic Tibia.	Styles. Seg. 9.	Styles. Seg. 8.	Antennae.	Cerci.	Appendix Dorsalis.
1st ..	2.9	0.130	0.210	..	..	1.16	0.505	0.72
2nd ..	3.4	0.160	0.265	..	..	2.35	1.04	1.52
3rd ..	4.4	0.176	0.312	..	..	2.78	..	..
4th ..	4.8	0.184	0.360	0.107	..	3.3	1.87	2.75
5th ..	4.8	0.206	0.404	0.252	..	3.9	..	..
6th ..	4.9	0.232	0.402	0.338	..	4.0	..	..
7th ..	5.5	0.244	0.501	0.396	..	4.5	2.8	3.8
8th ..	5.7	0.264	0.566	0.470	..	5.3	3.1	..
9th ..	7.0	0.287	0.624	0.532	0.160	5.6	3.7	4.5
10th ..	7.2	0.294	0.678	0.617	0.210	6.1	3.9	5.4
11th ..	7.8	0.325	0.747	0.699	0.291	..	..	6.0
12th ..	8.0	0.356	0.833	0.745	0.451	7.9	5.6	6.0
13th ..	9.7	0.373	0.904	0.856	0.571	8.5	6.5	8.5
14th . (Last Observed)	9.4	0.421	0.985	0.902	0.586	10.4	6.9	8.5

for the two sexes have been averaged together; for, although in the mature insects the relative lengths in the two sexes is different, the ratio being 1 : 1.56 for the male and 1 : 1.46 for the female, no consistent difference was found in these early instars.

There are also characteristic changes which enable certain instars to be distinguished fairly easily. Among these may be mentioned the following:—

The first instar is a pale cream colour without hairs or scales. The appendages are soft and relatively short, and the anus appears to be closed.

The second instar is a darker cream. The chitin is firmer and the appendages are longer and can be freely vibrated by the insect. A few bristles mark the position of most of the "brushes" of the adult. [The number of bristles increases in

the following instars and the bristle pattern may be found to be characteristic for each instar (cf. Buxton, 1938). The articulations are distinct even after the bristles have been lost. The patterns were however not studied in detail as it was realized that the size of the selected organs seemed to give an easier indication of an instar.]

The third instar is very active. It is dark cream in colour with purple tinting on the edges of the thoracic terga and the anal lobes. This colour persists in the succeeding instars.

The first three instars can be distinguished also by the tarsal segments. Each leg of the newly hatched insect has two tarsal segments. In the next instar, however, a septum develops on the second tarsal segment of the third leg, and in the third instar all the tarsi are three-segmented as in the adult.

In the fourth instar the scales are present. In this instar also the styles first appear, one pair being developed on the ninth sternum. They are "stubby" with many transverse "wrinkles." (The second pair of styles, which develops on the eighth sternum, does not appear until the ninth instar in the male and the eleventh instar in the female.)

It is interesting to note that the development during the first four instars resembles that of *Thermobia domestica* as described by Adams (1933).

In the fifth, sixth and seventh instars no particular distinguishing characters could be recognized.

In the eighth instar the genitalia first appear (fig. 5). They develop as two small lobes on the intersegmental membrane at the base of the cleft in the ninth sternum. This cleft first appears on the second instar, and becomes more and more marked until,

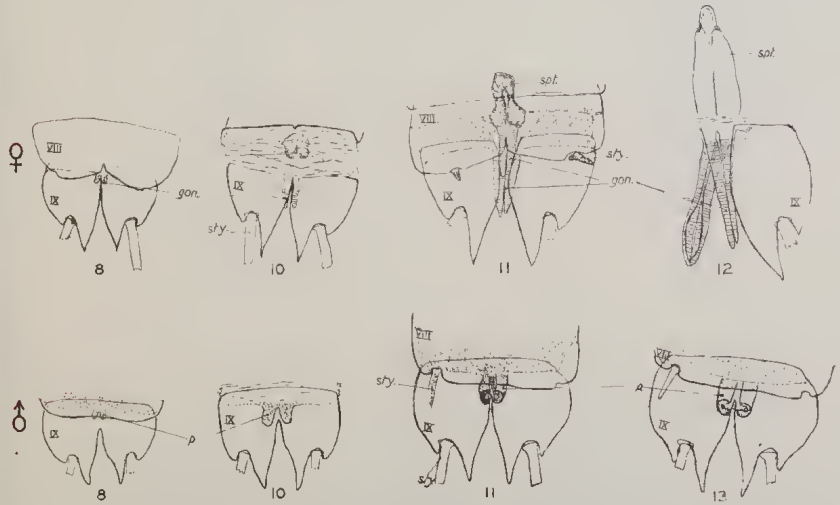

FIG. 5.—The genitalia of the young nymphs—ventral view; female 8th, 10th, 11th, and 12th instars; male 8th, 10th, 11th, and 13th instars; *gon.* gonopophyses; *p.* penis; *spt.* spermatheca; *sty.* styles.

in the eighth instar, the two sexes can be distinguished by its shape. The two sexes can be further distinguished by the small cleft in the eighth sternum of the female, which also develops in the early instars and extends deeper in the successive instars until this sternum, too, is completely divided.

In the males these two lobes remain short until by the eleventh instar the shape of the penis can be distinguished. By this stage too the internal organs have formed. The reproductive organs of the adult male are shown in fig. 6A. In the nymphs the various parts can be distinguished. There are seven large testicles: the vasa deferentia are short, thin-walled, and slightly dilated at the distal end, and the two fuse immediately anterior to the penis. In the next instar they lengthen and form two loops between the two nerves of the cerci. In the thirteenth instar the vesiculae seminales form, and the rolled edges of the penis fuse ventrally so that this now has the same form as in the adult.

In the female the lobes elongate and in the tenth instar a second pair develops from the membrane between the eighth and ninth segments. In the eleventh instar the posterior lobes

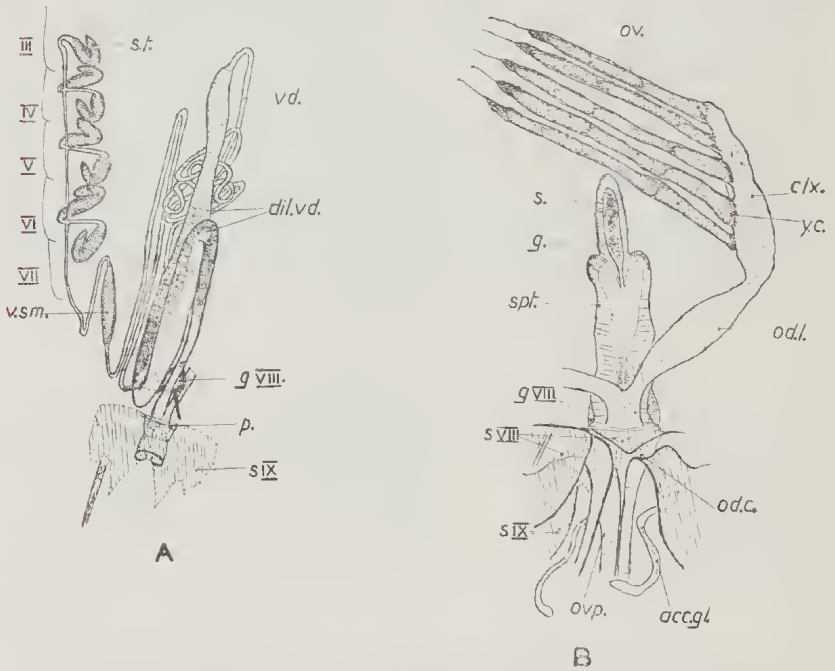

FIG. 6.—Reproductive organs of adult male *A*. and female *B*. (ventral view).
MALE:—*dil.vd.* dilated part of vas deferens; *gVIII* 8th ganglion; *p.* penis; *sIX* 9th sternum; *s.t.* sperm tube; *v.sm.* vesicula seminalis.
FEMALE:—*acc.gl.* accessory glands; *clx.* calyx; *gVIII* 8th ganglion; *od.c.* oviductus communis; *od.l.* oviductus lateralis; *ov.* ovariole; *ovp.* ovipositor; *s.* sperm, and *g.* granulated material in anterior prolongation of spermatheca, *spt.*; *t.f.* terminal filament; *y.c.* yellow cells.

elongate to within about 0.14 mm. of the points of the sternum, and the anterior pair extends ventrally to the base of the cleft in the ninth sternum. In the next instar the anterior pair are only a little shorter than the posterior pair, which now extend to within 0.08 mm. of the points of the sternum. In the thirteenth instar the two dorsal (posterior) lobes fuse and interlock with the two ventral (anterior) lobes as in the adult and the complete ovipositor projects about 1.2 mm. beyond the sternum.

At the same time the spermatheca develops. It appears first in the tenth instar as a short lobe directed anteriorly from the gonopophyses. In the twelfth instar it is already 0.6 mm. long and though the walls are still thin and undifferentiated, the two side sacs and the central neck are indicated (fig. 5). In the next instar the spermatheca has developed further and though it is still soft, the anterior prolongation, the neck region, and the two lateral pouches have well marked walls.

The internal reproductive organs have also formed by the thirteenth instar although the accessory glands and the "yellow" glands are not yet pigmented. The ovarioles still contain many small cells, the ova being not yet differentiated. The form of the organs in the adult female is shown in fig. 6B.

The detailed examination of the instars was not continued further than the fourteenth instar, as a preliminary examination showed that later development was concerned only with a very gradual increase in size.

In view of the extensive studies of growth rates which other workers have made, it is interesting to analyse the measurements of the instars of the silverfish in the same way.

The percentage increase in the average dimensions of the organs in the successive instars is shown in Table III. and it will be seen that this percentage increase is fairly constant, except during the first few instars. Apparently at its first appearance the organ is not as fully developed as is consistent with the later growth increments.

TABLE III.—RELATIVE INCREASE IN LENGTH OF PALPS, TIBIAE, AND STYLES FOR THE FIRST 14 INSTARS.

Instars.	Percentage Increase in Length.		
	5th Segment Maxillary Palp.	Metathoracic Tibia.	Styles of 9th Sternum.
1–2	123	126	..
2–3	110	118	..
3–4	105	115	..
4–5	112	112	235
5–6	113	114	135
6–7	105	108	114
7–8	108	113	117
8–9	109	110	119
9–10	110	109	113
10–11	110	110	116
11–12	105	111	113
12–13	113	108	106
13–14	..	109	115

Measurements were also made of the adult insects, comparing the organs of one side which were removed with those of the other side after the ecdysis. Although the adult insects increase in size over a period of several years, no regular increase in the size of these organs was observed, and in some cases they were the same size or smaller than those of the other side in the previous instar. Part of this discrepancy was probably due to regeneration.

The growth co-efficient (Huxley, 1932) of an organ is generally found by measuring its increase relative to that of the body when expressed by the formula:—

$$y = bx^{a}$$

where y is the size of the body; x is the size of the organ; b is a constant and a is the growth co-efficient.

i.e., the graph of log. (size of body) against log. (size of organ) is a straight line of slope.

Since the growth co-efficients of any two organs can be represented in this way, the relative growth of the two organs must follow the same type of curve. The relative growth of the palp and styles was compared with that of the metathoracic tibia, and the value of a for the palp was found to be 0.8, and for the styles 1.48. The same growth rates seem to be maintained until maturity. In fig. 7 the measurements of the individuals of three instars are shown. There is an almost continuous gradation in size between the instars, which is only to be expected when so many ecdyses are concerned in the growth of a nymph so similar in form to the adult.

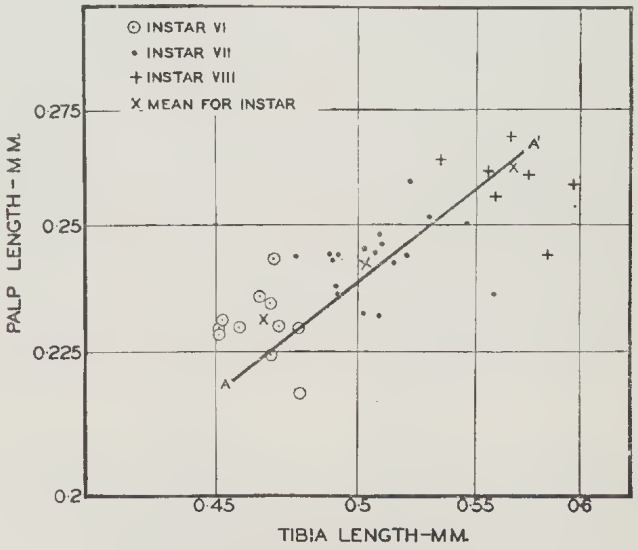

Fig. 7.—Variation in length of palp with length of tibia for three successive instars. Plotted on log-log scale. The slope of A-A¹ is the growth co-efficient of first 14 instars.

3. The Adult.

Ecdysis and Feeding:—Ecdysis continues after the silverfish reach sexual maturity. The relation of ecdysis to feeding was followed by observing the daily feeding of twenty individuals maintained at 24°C. In every case the insects did not feed during the last third of the stadium. During the first portion of the stadium they fed actively, although usually, there was a short period of one to three days before feeding began. These periods of no feeding presumably allow time for the old chitinous lining of the alimentary canal to be shed and the new one formed. (See p. 46.)

The insects which are found at night crawling about the floors and walls are usally in this feeding period of the early portion of the stadium. A number of these insects were collected and the rate of moulting watched; for example, one group of eighty-two insects collected on March 8th, 1937, started to moult ten days after capture (fig. 8). This continued for 60 days, when the last insect moulted. In another group of 30 insects caught on the 27th July, 1937, the same thing was observed; but, in this group, the last ecdysis did not occur until more than 100 days after capture. About 80 days after capture (October) the numbers of insects moulting greatly increased, probably because of the increasing room temperatures.

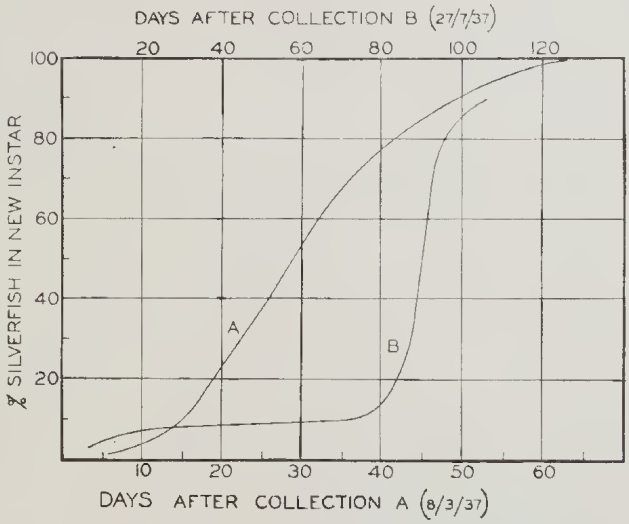

Fig. 8.—Length of time after capture before ecdysis occurred. Note the effect of increasing room temperatures in the rapid ecdysis in October of the insects collected 27.7.37. (Graph B.) The time scales of the two graphs are different.

Ecdysis:—The approach of ecdysis can be seen by the darkening of the new scales beneath the cream chitin of the old cuticula, from which, by the end of the stadium, most of the scales have been rubbed. This darkening increases during the last two to

three days of the stadium. When the new cuticula is completely formed, the insect starts to work the abdomen gradually forward until free of the last two segments of the old cuticula. Ecdysis then proceeds more rapidly. The abdomen expands and contracts; a deep furrow develops in the mid-dorsal line of the thorax and along the epicranial suture; the head is bent ventrally with the antennae and legs directed posteriorly, and the thorax is "hunched" until the furrows split. The head is dragged free, followed by the antennae and legs, and the cuticula is worked off the end of the abdomen. This part of the ecdysis is completed in ten to fifteen minutes.

The linings of the crop, gizzard, hind intestine and spermatheca are cast at the same time. Dissections showed that even before the new cuticula had formed, the lining of the crop and hind intestine were free in the lumen of the alimentary canal. The crop lining was broken off at the pharynx and with the lining of the gizzard passed back with the faeces.

It may be noted that in most insects the crop lining is cast through the mouth. In the case of the silverfish, the crop remains attached to the gizzard, and casting through the mouth is prevented by the arrangement of the large teeth of the gizzard. These can, however, be pushed backwards through a narrow opening for they fold into one another.

Under experimental conditions it was noticed that the silverfish were very slow-moving during the last days of the stadium. At this time, and during ecdysis they were readily attacked by other silverfish (particularly if the diet was not adequate). The exuviae were often eaten. Under unfavourable conditions it often happened that the insects died when the first split developed, or else they failed to draw the thorax out of the cuticle which then broke at the anterior end of the abdomen.

Mating and Egg Laying:—The cycle of growth and ecdysis influences mating and egg laying. The two sexes occur in about equal numbers. The spermatophore is probably formed at the time of copulation. It consists of a loose bag (1.5 mm. diameter) enclosing a coiled tube which ends on a long neck and pointed cap. It is presumably formed by the vasa deferentia of both sides (fig. 6) for the vas deferens of one side never seemed to contain fewer sperm or less gelatinous material, as might have been expected if the spermatophore were formed by one side only.

The neck of the spermatophore is pushed through the vagina into the body of the spermatheca, the tip fitting into the base of the anterior prolongation. The sperm are passed forward into the prolongation, preceded by a mass of finely granulated material. The female then eats the spermatophore from the base of the ovipositor, and in less than fifteen minutes there is no longer external evidence that mating has occurred. Copulation has not been observed but it is difficult to see how the long neck

of the spermatophore could get into the vagina of the female unless transferred directly by the male. (Compare Sweetman, 1938).

The chitinous lining of the spermatheca is always thick in the fertilized females; but whether this is merely due to age, or whether it is due to the stimulation of mating is not known. The posterior part of the prolongation of the spermatheca is closely constricted and must relax to permit movement of the sperm. There is also another constriction at the base of the body of the spermatheca. This is distended by the entrance of the spermatophore.

Mating probably occurs after each ecdysis as the contents of the spermatheca are lost when its lining is cast. On several occasions it was noticed that the females bearing spermatophores were in the early part of their stadium. The stage of development of the eggs at mating does not seem to be important, for sperm were found in the spermatheca of females with either medium sized or large eggs, and in other females containing large eggs no sperm were found. Females isolated from males continued to lay fertile eggs until ecdysis. The eggs laid after this soon turned yellow and shrivelled. Usually two or three batches were laid after the separation and then the females continued to live for two years apparently quite normally, but laid no more eggs.

The stimulus for the formation of the spermatophore is not known, but it is not a seasonal process. Dissections of males throughout the year revealed that the vesiculae seminales always contained active sperm, and on one occasion—in June, 1938—a number of insects were transferred from room temperature (about 10°C.) to 24°C. and several spermatophores were formed overnight. Apparently the males were in a condition to function as soon as the temperatures increased.

The length of time the eggs take to develop in the ovarioles is not known, but the development is not seasonal. Both large and small eggs were found in the ovarioles in both winter and summer. The lower two or three eggs apparently mature at the same rate in each of the ovarioles, and development proceeds at the same rate in the two ovaries.

An attempt was made to watch the rate of egg laying of isolated pairs of adult insects and of groups of three or four insects—220 in all—but very few eggs were laid under these conditions and the males were frequently eaten by the females. Dissections showed that the females contained nearly mature eggs but there was no evidence that copulation had occurred. This is in accord with the observations of Sweetman (1938), who found that several males were necessary to stimulate the act of copulation.

Another series of observations was made on 124 females and 96 males held in groups of 10 to 40 insects. These were watched

from February, 1937, to June, 1939, and during this time 4,573 eggs were laid (during this period 34 females and 24 males died or were removed). The average number of eggs laid per year by each female was 56. This occurred mainly in the summer, between the end of November and the middle of March, but a comparison of the rate of egg laying over the whole period showed some relation to room temperatures; for example, in 1938, egg laying continued until July, during which time the temperature was higher than in 1937. Again in March, 1939, higher temperatures resulted in greater egg laying.

V. The Effects of Temperature and Humidity.

1. Temperature.

Length of Stadium:—The effect of temperature on the length of the adult stadia, on the nymphs, and on the eggs was tested. The apparatus used was the multiple temperature incubator developed by Andrewartha (1935) for Thrips, and provided ten different temperatures. The temperatures of the insect containers were affected by outside temperatures to some extent, and it was necessary to calculate from the daily readings the mean temperatures for any period under consideration. The insects were provided with the standard diet (p. 36) and the humidity in each container was controlled by a 4 per cent. solution of sulphuric acid. This kept a relative humidity of about 96 per cent. and prevented the growth of moulds which became troublesome at higher humidities. Other experiments showed that the insects were not affected as long as the relative humidity was above 50 per cent.

In the final tests 39 insects were used and the average temperature was calculated for the period of each instar. These temperatures were then grouped into intervals of 1°C. and the mean length of the stadium for the temperature interval was calculated. Although the insects used were of about the same size, there was considerable variation in the lengths of stadia (Table IV.). However, the average lengths of the stadia showed clearly the increasing rate of growth at temperatures above 16°C. The greater activity above 20°C. was also evident from the rapidity with which the food was consumed.

Table IV.—Average Length of Adult Stadia at Various Temperatures.

Temperature °C.	Average Length Stadium.	Range.	Number of Insects.	Temperature °C.	Average Length Stadium.	Range.	Number of Insects.
	Days.	Days.			Days.	Days.	
29	15	..	2	22	43	30–58	4
28	17	20–15	2	21	46	38–65	6
27	30	13–44	10	20	67	49–106	11
26	40	35–46	2	18	59	50–68	2
25	39	24–50	8	16	129	121–142	4
24	51	36–79	3	15	165	100–239	4
23	37	21–46	6	14	220	106–263	4

The eggs and young nymphs were also subjected to a range of temperatures (Table V.). The individual rates of development were uniform for the egg and the first two instars.

Table V.—Average Length of Hatching Period and 1st Stadium at Various Temperatures.

Temperature °C.	Period of Hatching.	Length of First Stadium.
	Days.	Days.
29·5	20	5
25·3	27	5
25·0	30	5
24·0	34	5
23·0	46	7
21·0	49	9

At temperatures below 13°C. the insects became torpid, and at 11°C. ecdysis stopped even if the cuticula had been partly shed. However, the process was completed when, a week later, the insects were put in a temperature of 24°C. Adult insects survived several months at 1°C. but second instar nymphs were killed in two days by the low temperature and at 11°C. survived for only twenty-five days. At 12°C. the length of life increased to seventy days.

Length of the Life Cycle:—In Melbourne, the life cycle extends over several years. Owing to some difficulty during the first year in providing a supply of food adequate for growth, insects have not yet been reared from egg to maturity. However, the total length of the life cycle can be estimated from observations of different periods. For example, in November, 1937, thirteen nymphs 4 to 10 mm. long were collected in the laboratory. These had probably developed from eggs laid the previous summer. By November, 1938, they had grown 10 to 12½ mm. and some laid eggs during the first week of December, 1938.

Under the conditions maintained for the stock insects (24°C.), eggs hatched in 34 days, the nymphs reached the thirteenth instar, 9½ mm. in eleven months, and would probably reach sexual maturity in eighteen months. At this temperature egg laying continued throughout the year.

It is interesting to compare these conditions with those maintained for *Thermobia domestica* (Sweetman, 1938).

Activity and Distribution:—These results obtained under controlled conditions may be compared with observations of the insect's normal activity. It is assumed that the mean air temperatures give a measure of the conditions obtaining in the insects' microclimate.

The prevalence of silverfish in the capital cities as judged from the reports of residents, pest destroying firms, and the Government Entomologists, can be related to the length of the period the temperatures are above 16°C., the limiting temperature

for active feeding and growing. It is only in those places which have long periods of temperature higher than 16°C. that the silverfish can increase to pest numbers. In a brick or stone house an indoor temperature of 16°C. normally corresponds to an outside temperature of about 55°F. (data received from the Commonwealth Meteorological Bureau, Melbourne). For example, the average daily temperatures were above this limit in Hobart for six and a half months, and Brisbane for the whole year. Very high temperatures do not limit the distribution of the silverfish in Australia, for air temperatures do not persist long enough above 30°C. to cause death.

The activity of the silverfish during the year in Melbourne can be related to the air temperature. During the winter months the metabolism is slow. Digestion proceeds slowly and observations on the stock insects showed that even some days after feeding, the crops still held many large fragments of digestible material. Since the need for food is reduced, the silverfish are seldom to be found at night on the walls and floors. For example, 25 weekly collections at 10 p.m. were made in one building during the period May to November, 1937. The average winter catch was fifteen, but during October, the number caught increased to 80. In all, 770 large insects were collected during this period.

These figures give an indication of the number of silverfish in a building which was not considered to be very badly infested. An occasional spraying was the only control used. Evidently

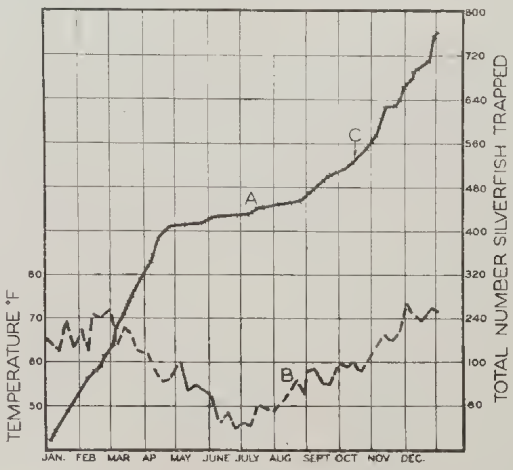

Fig. 9.—Influence of temperature on activity of silverfish. A. Progressive total of silverfish trapped in the sinks in one laboratory during 1937. The sinks were cleared each day. From October (point C) collections in other places also greatly increased. B. Mean weekly temperatures.

not all the insects are ranging on the walls and floors at the same time; for after an exhaustive search on four successive nights in October the same number of insects were caught on each occasion.

The number of insects accidently trapped in the sinks in one laboratory showed this same increase as the weather became warmer (fig. 9). Daily counts were made during 1936 and 1937, and, in both years, the numbers trapped increased greatly after October, when the mean weekly temperatures increased from 12.8° to 15.9°C.

High Temperatures:—The increased activity at higher temperatures continues to about 24°C.; but, temperatures higher than this are fatal, death occurring after a period which decreases from several months at 26°C. to one hour at about 41°C. (Table VI.). The effect of high temperature on other species of insect has been studied by many other workers (e.g., Buxton, 1931; Mellanby, 1932) with particular reference to the effect of moist and dry air, and to the possibility of some regulation of body temperature by the insect, at least, for short periods.

Table VI.—Minimum Period of Exposure at High Temperatures.

Temperature °C.	Period of Survival.	Number of Insects.
41·5	1 hour	9
40·0	15 hours	9
33·6	6 days	1
33·1	9½ ,,	4
32·6	9 ,,	6
31·3	24 ,,	2
31·0	16 ,,	2
30·1	8 ,,	7
29·5	21 ,,	5
29·0	11 ,,	2
26·0	4 months	10

These results were obtained in the multiple temperature incubator during the tests on maximum lethal temperatures.

The tests on silverfish were carried out by placing the insects in a test tube (2 in. x ¼ in.) suspended in a Florence flask in which humidities of 5 per cent. and 85 per cent. were maintained by solutions of sulphuric acid. The introduction of the silverfish through a tapering glass tube lowered the temperature of the flask, which required 30 minutes to return to that of the water bath in which it was immersed. The bath temperature was maintained to within ± 0.02°C. and a correction of 0.25°C. was applied, when necessary, to allow for the initial temperature drop. About 250 insects were used. After preliminary tests, 24 groups of nine insects each were used to determine the lethal temperatures for exposures of one hour and fifteen hours respectively.

In addition sixteen tests were made with periods other than one hour and fifteen hours.

For exposures of one hour, the highest temperature at which all the insects survived was 41.5°C. At higher temperatures an increasingly greater percentage of the insects died; but the mortality was lower in the dry air (fig. 10). Similarly for exposures of fifteen hours, the highest temperature at which all the insects survived was 38.8°C. Presumably, even during the short exposure of one hour, the body temperature of the insect was reduced by evaporation of the body fluids, though this point was not checked by measuring the weight lost by the insects during the test. After exposures of fourteen hours the effect of evaporation was still appreciable, but, presumably, in still longer exposures, this loss of water would be so great that the lethal temperature would be lower in dry air owing to the desiccation of the insects.

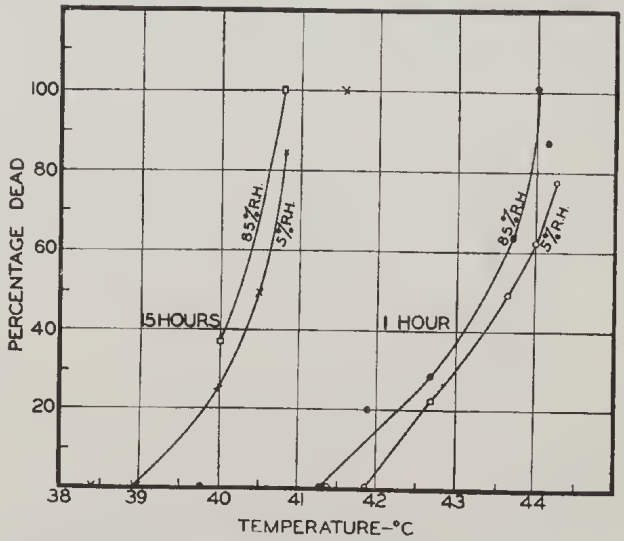

Fig. 10.—Lethal Temperatures for Exposures of one and fifteen hours in air of 85 per cent. and 5 per cent. Relative Humidity.

The variation in the reaction of the individual silverfish to the high temperatures is in accordance with that found in other insects. In the case of the silverfish, the variation was about the same in the two series of experiments, and was not greater in dry air as Buxton (1931) had found with *Rhodnius*.

In the third series of experiments, exposures of various periods were used, and those which caused the death of all the insects at the various temperatures (about five insects being used for each test) have been summarized in Table VII.

Table VII.—Maximum Period of Survival of Adults at High Temperatures.

Temperature °C.	Fatal Period.
45·0	30 mins.
44·0	40–45 „
43·8	60 „
42·4	75 „
41·5	15 hours
39·5	40 „
38·0	72 „

After the silverfish had been exposed to high temperatures for fifteen hours or more, there was no difficulty in determining which were dead; but after a short exposure many became merely torpid. Some died but others recovered during the next 24 hours (and behaved normally at subsequent ecdyses). To take these insects into account the percentage dead at each temperature was calculated from the number dead 24 hours after the end of the test.

During exposure to high temperatures the silverfish moved about very rapidly. As soon as they were lifted out of the thermostat to cool, they became torpid, but again moved about actively when put back into the high temperature enclosure. This could be repeated several times. Finally, after 24 hours at room temperature, some of the torpid insects recovered. This behaviour is interesting in view of the possible causes of the lethal effects of high temperature which Mellanby has suggested. The only visible effect of the high temperatures was associated with the fats. The large fat bodies on the dorsal wall of the abdomen became so clear in the dead insects that the internal organs could be seen through the thin chitin. This "clearing" did not occur in the insects which merely became torpid, or in the insects killed by exposures of fifteen hours and longer.

The fact that the lethal temperatures were higher in dry than in moist seemed to indicate that the insects had some control over their body temperature, and an attempt was made to measure their rate of heating after they had been transferred to a higher temperature.

The method used was that generally adopted, i.e., the piercing thermocouple (Robinson, 1928ii); but a consideration of results showed that the silverfish was so small that the temperature of the couple was determined by conduction along the wires rather than by the temperature of the insect itself. It was concluded that only in an insect above a minimum size (depending on the conductivity of the tissues), would the thermocouple be at the same temperature as the insect.

A still more serious drawback to the method was the unavoidable injury to the silverfish. Although the silverfish could live for longer than one week while impaled on the junction, provided the crop had not been pierced, they were susceptible to high

temperatures and died after an exposure of one hour at 30°C. It was therefore not possible to test temperatures so high that any control of the body temperature by the insect itself could be expected to operate.

For the calculation involved in determining the rate of heating it was desired to know the specific heat of the insect. A calorimetric determination was attempted but the rise in temperature, which continued for one hour, was too great to have been derived solely from the heat of the insects, and it seemed probable that it was partly due to the heat of wetting.

The high value for the Specific Heat (1.4) obtained from the figures of Bodenheimer and Schmidt (1931) may be due to the inclusion of this "heat of wetting" in the total rise in temperature. No indication of the rate of temperature rise was given.

2. The Effect of Humidity.

The silverfish takes no liquid but must obtain its water from that absorbed by the food, and from that produced by the oxidation of foodstuffs. There is no excessive loss from the alimentary canal because water is absorbed in the hind intestine and rectum and the faeces are dry when extruded; but there is a continual loss from the tracheal system. The tracheae open at ten spiracles (fig. 11A), which have no closing mechanism, but are protected to some extent by the folds of the intersegmental membranes on which they are situated (fig. 11B). This simple tracheal system and the thin cuticle make the silverfish particularly susceptible to dry conditions. The effect of a range of humidities was studied and an attempt was made to understand the water relations of the tissues, when death occurred from drying. For most of the tests, adult, early stadium insects were used.

Water Content:—The water content of normal silverfish was determined by—

(*a*) drying at 103°C.;
(*b*) ether extraction of fat and water from the fresh insects.

The average water content of 165 insects was 72.4 per cent. The agreement of the results from the two methods showed that drying at 103°C. caused no appreciable decomposition of the tissues although the insects became brown during the process.

The individual determinations varied between 70.5 per cent. and 82 per cent. water. Variations of this order have been found in other insects. In the silverfish this variation could not be correlated with the moisture content of the food (as Robinson, 1928, had found in the grain weevils) although the food varied from paper (7–8 per cent. water) to a mixed diet containing some fresh plant tissue.

The relationship between the water content and the body weight can be shown by curves on a log/log scale. The "k" value for the silverfish 0.96 compares with the values for both the mealworm 0.975, and the wax moth 0.96 (Huxley, 1932) and shows that there is no relative change in the water content with body weight.

Effect of Dry Air:—The insects survived only short periods in air over calcium chloride. The average length of life of 35 insects was thirteen days; but there was considerable variation, the extreme limits being three days and 26 days.

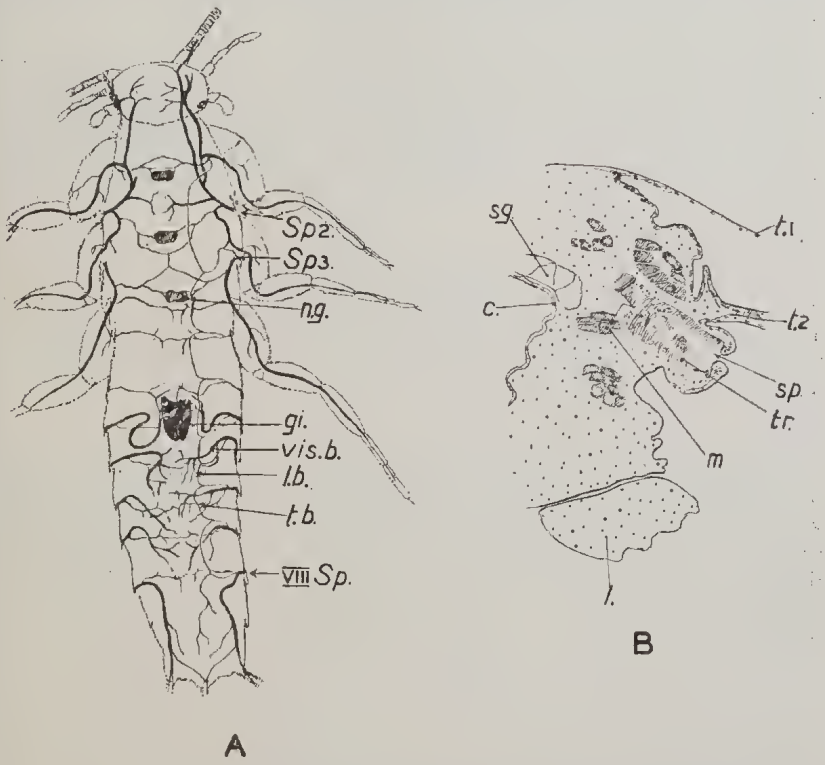

FIG. 11. TRACHEAL SYSTEM.—A. Dorsal View:—The dorsal system has been removed from the left side; *n.g.* nerve ganglion; *gi.* gizzard; *l.b.* lateral branch; *t.b.* transverse branch; *vis.b.* visceral branch. Sp_2, Sp_3, *VIIISp.* Spiracles of meso and meta thoracic segments and 8th abdominal segment.
B. Opening of 1st trachea:—Drawn from two successive sections 7μ. thick × 245; *l.* leg; *m.* muscle; *t1.t2.* terga I and II; *tr.* trachea; *sp.* spiracle; *s.g.* salivary gland; *c.* crop.

The rate of loss of water was determined from daily weighings of eighteen silverfish held at 24°C. Each insect was held in a small tube $\frac{1}{4}$ in. x $\frac{1}{2}$ in. Nine were fed and nine starved. Two of each lot were kept under stock conditions as controls. These and

the one survivor were killed at the end of the test of 24 days, and the dry weight of all the insects determined. The total weight of the faeces was 0.15–0.6 mg., and was included in the weight of the insects at each measurement.

The individual rates of loss showed considerable variation but there was no significant difference between the fed and starved groups. The metabolic losses are small under these confined conditions, and as Gunn (1933) has shown, the loss of weight may be taken as a measure of the loss of water. The silverfish died after losing 20 per cent. to 75 per cent. of their weight. The average loss per day was 4.6 per cent.

The period of survival could not be correlated either with the rate of loss of weight, with the percentage of water lost until death, or with the water content of the body at death. For this latter figure the whole weight of the body was used, as the weight of the chitin is relatively small. No attempt was made to consider the water content of special tissues as Mellanby has suggested (1937).

The rate of loss of weight gradually decreased towards the end of the period, but it was usually the same five days before and after death, i.e., death was not followed by a suddenly increased loss of water. Even in insects still more susceptible to drying, e.g., *Phlebotomus* larvae, Theodor (1936), the rate of loss of water did not change at death.

Comparison of the Loss from Insects at Different Times in the Stadia:—The loss of water from insects late in the stadium was compared with that from insects early in the stadium. The insects were starved throughout the tests. Although during the first three and a half days the rates of loss of weight of the two groups was the same, over the whole period the late stadium insects lost water more rapidly than those early in the stadium. Their total loss until death was 66 per cent. compared with 57 per cent. for the early stadium, and the water content of the tissues at death was lower, 53 per cent. compared with 62 per cent. for the early stadium. (A determination of other groups of insects from stock showed a water content of 74.1 per cent. for the late stadium compared with 73.2 per cent. for the early stadium.) The late stadium insects also survived for a shorter period, the mean length of life for the group being 12.4 days compared with 16.3 days for the early stadium insects.

The slower rate of loss from the early stadia was probably due to the added protection of the layer of scales which are rubbed off the thin cuticle later in the stadium.

Loss of Water at Ecdysis:—Ecdysis is accompanied by changes in weight which are probably due to changes in the water content of the body. Even in moist air the insects lost about 8 per cent.

of their body weight during the seven days preceding ecdysis. This loss continued during the day after ecdysis and then the weight slowly increased.

The insects are most susceptible to dry conditions during the period of ecdysis, and after about four days' exposure they were not able to complete the moult. Death occurred usually after the old cuticle had split along the thorax.

Effect of Various Humidities:—The various humidities were maintained in Mason jars by sulphuric acid solutions of the required concentration. The insects were held in small tubes suspended in the jars, and paper and casein were provided. The tests were made at room temperatures.

The critical humidity seems to be about 55 per cent. There was some evidence that the length of life decreased at very low humidities (Table VIII.), which evidence is supported by the fact

Table VIII.—Length of Life at Various Humidities.

Relative Humidity.	Number of Insects.	Period of Survival.	Range.
%		Days.	Days.
0–19	13	12	5–26
26–45	52	15	6–40
50–52	49	28	> 70
55	8	> 146	

that the rate of loss of weight was greater at the lower humidities (fig. 12, Table IX.). There was also some evidence that the length of life was shorter at higher temperatures for any given relative humidity.

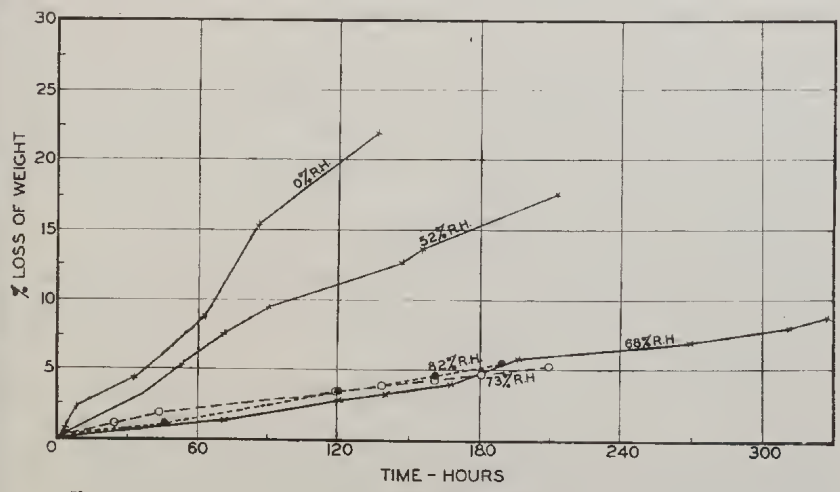

Fig. 12.—Rate of Decrease of Weight of System (Insects and Food) when held at various humidities.

Table IX.—Change in Weight of Insects Held at Various Humidities at About 18°C.

	Relative Humidity.			
	52 Per Cent.	68 Per Cent.	73 Per Cent.	82 Per Cent.
Initial weight (mg.)	353·7	338·4	253·5	382·3
Number of insects	13	13	14	15
Period of test (hours)	300	300	210	190
Total loss of weight of food and insects as percentage of initial weight	29·3	9·5	5·4	5·5
Food eaten (mg.)	11·1	33·9	12·5	35·7
Food eaten as percentage of initial weight of insects	3·1	10	4·9	9·3
Change in weight of insects as percentage of initial weight	−26	+0·5	−0·4	+3·8

The effect on recently laid eggs from stock insects was also tested. The nymphs survived at humidities above 55 per cent., but at lower humidities they died during the second ecdysis. At a relative humidity of 35 per cent. they died during the first ecdysis, and in dry air they failed to hatch, or died during the first instar.

When measuring the rate of loss of weight, new stadium insects were used, and were weighed separately from the food only at the beginning and end of test period. In the more humid conditions they ate sufficient food to maintain their body weight, and a relative humidity of 82 per cent. actually increased their weight by 4 per cent. In dry air they lost more weight than could be replaced from the food. Some general disturbance experienced in dry air may account for the low food consumption, and for the fact that their length of life was not increased by feeding.

Absorption from Moist Air:—Under natural conditions silverfish are not subject to dry conditions for long periods. The fact that they survived for some months when subjected to dry periods of 1, 4, and 7 days with intervening periods of one day in moist air, indicated that they could absorb moisture from the moist air. Preliminary tests indicated that the increase in weight of partly desiccated insects was proportional to their loss in weight during the preceding period in dry air. Insects which were collected while freely ranging on the walls, did not change in weight during a period of five days in moist air.

In subsequent experiments, the insects were held in dry air for various periods, and then left for four hours in air of 99 per cent. relative humidity. Every care was taken to eliminate condensation, so that the change in weight might be due only to absorption from the air.

A 300-cc. Florence flask containing 20 ccs. of 2.3 per cent. sulphuric acid was immersed to the stopper in a water bath which was maintained at 23.5°C. ± 0.02°C. Three small glass vials $2\frac{1}{2}$ in. x $\frac{1}{2}$ in. were suspended in the flask by wires. After the insects had been kept in the dry air for the required period, they

were rapidly run into one of the vials through a small glass funnel and rested on a small piece of rubber in the bottom of the tube. After four hours they were transferred to closed weighing bottles and weighed immediately, and again after drying at 103°C. for six hours.

Table X.—The Absorption of Water from Moist Air at 23.5°C.

Previous History.	Dry Weight.	Change as Percentage of Dry Weight.	Initial Water Content Percentage.
	mg.		
From stock	36·9	− 1·1	75·4
From stock	41·9	− 0·2	72·4
In moist air, 96 hours	43·9	− 1·8	71·9
Desiccated, 4 hours	40·3	− 4·6	71·2
Desiccated, 15 hours	39·0	+ 2·1	70·9
Desiccated, 72 hours	35·4	+ 2·8	73·5
Desiccated, 96 hours	48·1	+ 3·9	69·4
Desiccated, 119 hours	34·5	+ 4·1	71·4
Desiccated, 144 hours	39·7	+ 1·5	73·0

In all but two experiments, the increase in weight was proportional to the length of the previous desiccation (Table X.). It was thought that the water content of the tissues after desiccation ("initial water content" in Table X.) would depend inversely on the length of the period of desiccation, but no such relationship was found, probably because there was some variation in the amount of food consumed during this period, with consequent variations in the amount of the water loss replaced from the food. The change in weight of insects from moist air (maintained with a dish of water in a closed tin 12 in. x 9 in. x 6 in.) was measured for comparison. These actually decreased in weight. Insects from stock suffered little change in weight, which shows that under the stock conditions they maintain a water content which is in equilibrium with an air of 99 per cent. relative humidity.

Humidity Preference.—With certain experiments it was necessary to provide a supply of moisture by means of a cotton plug in an inverted tube of water. In the open vessels the silverfish congregated on this wet surface; but in the closed vessels, the humidity was raised, and they no longer rested on the plugs.

An attempt was made to measure their response to a humidity gradient. The method recommended by Gunn, 1936, was used, but the extreme limits of humidity achieved by water and concentrated sulphuric acid, was 44 per cent. to 64 per cent. with 56 per cent. in the middle (as measured by a humatograph). The silverfish showed no preference for any region, even after the tests had been continued for one week.

Discussion:—These experiments show that silverfish are fairly susceptible to dry conditions, and that they derive at least part of their water from moist air.

No definite information about the water relation of the tissues at the time of death from desiccation could be obtained. The figure of most value seemed to be the "water content of the tissues at death." All the various species studied by other workers died when the water content of the tissues was reduced to 53–62 per cent., even though the different species lived in dry air for very different lengths of time. However, the water content at death of individual silverfish varied within still wider limits, 30–76 per cent., and even the individuals which survived desiccation the longest showed no closer similarity in this, or in the rate of loss of weight during the last days of life.

Though adaptation to dry conditions might not be expected, there seemed to be, at the higher humidities, some relationship between the amount of food eaten and the loss of weight. In air drier than 52 per cent. relative humidity the water lost was not replaced from the food eaten, but rather, less food was eaten than at the higher humidities. Buxton found that in starving meal-worms, the metabolism of dry matter was proportional to the loss of water, and the water content of the tissues remained constant. He considered this to be an adaptation to dry conditions; but later experiments with a wider range of insects showed that this could not be generalized and Mellanby, 1936, showed that metabolism is controlled solely by temperature and not by humidity.

Since the insects can take up moisture from a humid atmosphere, and since they tend to congregate near moist surfaces, dryness is probably not a limiting factor under natural conditions. Even at 60 per cent. relative humidity the loss of water was only 0.14 mg. per day.

VI. Nocturnal Habits.

Under natural conditions the silverfish feed at night. Shortly after dusk (approximately 8 p.m. in summer and 6 p.m. in winter) they emerge from the crevices of a room and move about the floor and walls usually in short runs with long pauses between. At daybreak, they return to the crevices again. They seem to be able to find shelter very easily, and, when disturbed at night by a bright light, they turn about and seek the crevice from which, presumably, they have emerged. If far from the wall, they seem to make short runs in random directions, but even then, they usually reach cover within ten minutes. This reaction to light was watched during both day and night in half-covered petri dishes some of which were exposed to strong artificial light.

The insects in the illuminated dishes always sheltered in the shaded part. During the day, even in the completely shaded dishes, the insects only occasionally moved about and fed; but as dusk fell, they moved about and fed even in the illuminated dishes.

When suddenly illuminated, the insects, after a pause of about half a minute, started to move their antennae actively. After one to two minutes they started to move about. By the end of seven minutes they reached the shadow of the piece of paper in the dish, and did not move into the light again.

Besides avoiding light in this way, the silverfish took shelter in a crevice between two glass slides and remained there quietly although they were still exposed to the light.

VII. Spraying.

The nocturnal habits of the silverfish are important in determining the effectiveness of the use of sprays as a means of control, for the insects sheltering in the crevices can seldom be reached by the spray. The vapour alone of a kerosene-lethane-pyrethrum mixture is not lethal so that they are not killed unless they come in contact with the spray droplets or the sprayed surface. In one test a cupboard of 170 c.dm. capacity was sprayed at the rate of 1 cc. per 40 c.dm. This was sufficient to make a very strong smell, but did not kill the silverfish in a petri dish protected from the falling spray by a sheet of filter paper which was removed ten minutes after the spraying.

The toxic effect of the spray on wood persisted for some hours. It was noticed that for four to six hours after the spraying of a room had been completed, dead insects could still be collected. In some cases these had crawled 3 feet to 4 feet beyond the sprayed area. The persistence of the toxic effect of the sprayed wood was further tested by confining silverfish at intervals on the surface of pieces of wood which were sprayed with a measured amount of fluid.

After a spraying of 1cc. per 14 c.dm. the insects were killed by four minutes' contact with the wood, two and a half hours after spraying. Even after the wood had been kept three days in the closed cupboard, the insects were killed by being confined on its surface for another two days.

Spraying therefore is most effective if done at night, and if at least one foot of the surface around the crevices is made thoroughly wet so that the insects cannot escape from the sprayed areas during their first moments of stimulated activity.

Both *C. longicaudata* and *L. saccharina* were used in the spray tests. *C. longicaudata* suffered a higher mortality because the torpid insects exuded a small drop of fluid from the mouth. This coagulated and fixed the head to the surface so that even when the insect recovered it could not get free.

The lethal effect of Paradichlorbenzene ("P.D.B.") and naphthalene depended on the vapour and not on contact with the insect.

VIII. Conclusion.

Whether *C. longicaudata* is a native of Australia is not known, but it is now widely distributed and it is the only one of the many silverfish in Australia which occurs in great numbers in buildings. *Thermobia domestica* Pack. and *Lepisma saccharina* L., the two common silverfish of Europe and North America are also found here, but large numbers occur only in isolated habitats.

Though the rate of egg laying is comparatively low, the long life of the adults leads to a rapid increase in numbers. For example, assuming that each female lays 56 eggs per year and that there are no fatalities, the progeny of one pair would lay 470,000 in the seventh year.

Climatic conditions in most parts of Australia are favourable for rapid development, and by its nocturnal habits, it escapes the most severe periods of heat and dryness.

It feeds on a wide variety of materials and ranges far in search of food, and probably under normal conditions lack of food does not limit its development. No natural control appears to operate and it seems that artificial control methods must be continuously applied to protect particular articles and to reduce the numbers of the insects.

IX. Summary.

The long-tailed silverfish, *C. longicaudata,* is widely distributed in Australia and is becoming a pest of increasing importance.

It is a general feeder, eating plant and animal remains as well as commercial goods such as papers, wallpapers, and artificial silk. The selective attack on wallpaper and writing and printing paper is due to the palatability of certain constituents. In wallpaper the palatable materials are the starch and dextrin sizes which are mixed with the pigment to produce the thick coloured layer on the face of the paper. In writing paper the palatable material is the chemical pulp containing degraded celluloses. Papers containing more than 45 per cent. mechanical pulp are not eaten and the unpalatable materials in this pulp are associated with the " ether extract " fraction.

The surface of papers and artificial silk can be rendered unpalatable by spraying with a 1 per cent. solution of tricresylphosphate in a petroleum solvent (" White Spirits ").

Digestion occurs mainly in the large crop, where the action of the gizzard is supplemented by that of cellulose digesting bacteria, and by enzymes which pass forward from the mid-intestine.

The pH of the successive regions of the alimentary canal was found by feeding the insects with indicators and noting their colour in the intestine.

Methylene blue and Sudan III were absorbed from the mid-intestine and showed that there were three distinct regions in the epithelial lining. They also stained certain organs of the body and were finally removed by the malpighian tubules.

The life cycle from the egg to sexual maturity takes two and a half to three years and the adult insect continues to grow, moult, and lay eggs for at least four more years. The successive instars can be distinguished to some extent by the relative size of certain organs and by the state of development of the gonopophyses and reproductive organs.

The insect's activities are greatly affected by the periodic ecdyses. Feeding occurs only during the first part of each stadium. Fertilization occurs after each ecydsis. Egg laying occurs throughout the summer months and on the average 56 eggs are laid by each female each year.

Yeast and ground wheat provide an adequate diet for the development of the nymphs. Adult insects have survived for three years on a diet of paper only, and for nine months without any food.

Under experimental conditions active feeding and growth begin at about 16°C. The "optimum" is 25°C., and continuous exposure to temperatures higher than this cannot be survived for long periods. Below 11°C. development stops and the insects become torpid. The distribution of silverfish in Australia in pest numbers, and their activity during the year, can be related to air temperatures.

The lethal temperatures for exposures of one hour and fourteen hours are lower in dry than in moist air, and indicate some control of the body temperature by the evaporation of body fluids. Attempts were made to measure the body temperature with a thermocouple and to measure the specific heat of the tissues.

On the average adult insects live only thirteen days in dry air, during which time the water content of the tissues is reduced from 72 per cent. to 58 per cent. They are most susceptible to dry conditions during the period of ecdysis. Insects early in the stadium can survive a greater loss of water than insects late in the stadium. Humidities above 52 per cent. are not fatal, and the water lost is replaced from the food. The insects congregate on a damp surface but do not show any preference for air of 64 per cent. relative humidity over 44 per cent. relative

humidity. Partially dried insects take up water from moist air, so that the effect of short periods in dry air is not cumulative, provided that there are intervening periods in moist air.

Their nocturnal habits are important in determining the effectiveness of spraying as a means of control. They are killed by contact with the spray droplets, or with the sprayed surface on which the toxicity of the spray persists for several hours.

From the nature of the insect's life cycle, its feeding habits, its temperature and moisture requirements and the absence of natural enemies, it is concluded that control measures must be continuously applied to keep this species under reasonable control.

Acknowledgment.

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Appendix.

In the following table is summarized the behaviour of the various materials tested as deterrents. Usually 90 per cent. alcohol was used as the solvent, and the concentration measured in grams per cc. of solvent or else a saturated solution (S) was used. Although several concentrations of each material were tested, only the behaviour of the most concentrated solution of each is included in the table.

In some cases the decomposition of the material was appreciable only after the sprayed paper had been exposed to sunlight for two weeks. This decomposition was evident by the discoloration of the paper, or by the subsequent ready attack by the silverfish. Some of the materials acted as stomach poisons and others proved toxic before the paper was eaten. During the tests the insects were confined on the surface of the sample or were held in a closed vessel (3 in. x 6 in. x 12 in. high) so that the toxicity was caused either by contact or by the vapour. In such cases new groups of insects were used, after the paper had been exposed to the air. The effect of the vapour alone was investigated only for mercuric chloride. Paper sprayed with this material caused the death of silverfish held in a test tube, when supported 1 in. above the insects so that it was out of reach.

Material.	Concentration.	First Attack Days.	Toxic. When Eaten.	Toxic. Without Eating.	Decomposes or Volatile.	Discolours Paper.
Phenol Derivatives.						
Acetylsalicylic acid	S.	27	−	−	−	−
Acetylsalicylic acid (Sodium salt)	5%	27	−	−	−	−
Amylmetacresol	1%	60	−	+	+	+
Beechwood creosote	10%	2	−	−	−	−
Catechol	5%	27	−	−	−	−
Chlor. betanaphthylsalicylate	−	>240	−	−	−	+
Dibromobetanaphthol	S.	100	−	+	+	−
Dihydroxynaphthoic acid	S.	270	−	−	−	+
Dinitrophenol (2·4)	S.	27	−	−	−	−
Diiodothymol (Sodium salt)	S.	27	−	−	−	−
Diphenol	1%	27	−	−	−	+
Diphenylphenol	S.	35	−	+	+	−
Gallic acid	S.	4	−	−	−	−
"Hexol" disinfectant	−	70	−	−	−	−
Hexyl phenol	10%	180	−	+	+	−
Hexylresorcinol	1%	60	−	−	−	+
Hydroquinone	5%	27	−	−	−	−
Methylsalicylate	−	7	−	−	−	−
Metacresol	10%	20	−	+	−	−
Metacresol (Sodium salt)	10%	20	−	+	−	−
Metacresotinic acid (Sodium salt)	S.	−	−	−	+	+
Monochlorophenol (Sodium salt)	10%	70	−	−	−	+
Naphthol	S.	−	−	+	+	+
Parahydroxybenzaldehyde	5%	27	−	−	−	−
Parahydroxydiphenyl (Sodium salt)	S./2	20	−	−	−	−
Paranitrophenol	5%	−	−	+	+	+
Paranitrophenol (Sodium salt)	S	27	−	−	−	−
Paratertiaryamylphenol (Sodium salt)	2%	60	−	+	+	+
Paracyclohexylphenol (Sodium salt)	S.	>200	−	+	+	−
Resorcin	5%	27	−	−	−	+
Saligenin	S.	27	−	−	−	−
Sulphosalicylic acid	5%	30	+	−	−	−
Sulphosalicylic acid (Sodium salt)	S.	60	−	−	−	+
Tannic acid	4%	30	−	+	+	+
Thiodiphenylamine	S.	−	−	−	−	+
Thymol	S.	60	−	+	+	+
Tricresylphosphate	1%	−	−	−	−	−
Tribromphenol	S.	180	−	+	+	+
Other Compounds.						
Abietic acid	S.	14	−	−	−	−
Aloes	S.	40	−	−	−	−
Ammoniacum	S.	14	−	−	−	−
Aluminium chloride	4%	35	−	−	−	−
Antimony sulphate	S.	15	−	−	−	−
Anthracene	S.	15	−	−	−	−
Barium oxalate	S.	31	−	−	−	−
Barium thiosulphate	S.	5	−	−	−	−
Borax	17%	13	−	−	−	−
Cetyltrimethylammonium bromide	−	1	−	−	−	−
Citronella	−	60	−	−	−	−
Copal	S.	14	−	−	−	−
Malic acid	5%	17	−	−	−	−
Mercuric chloride	0·5%	30	+	−	−	−
Mercuric cyanide	S./4	30	+	−	−	−
Mercurochrome	0·3%	14	+	−	−	+
Mercurosal	1%	50	+	−	−	−
Metaphen	0·2%	20	+	−	−	−
Pyridine	5%	2	−	−	−	−
Sea Water soap	−	4	−	−	−	−
Sodium fluoride	S.	26	+	−	−	−
Stannous ammonium chloride	4%	20	−	−	−	−
Stannous chloride	S.	25	−	−	−	−
Tartar emetic	S.	>240	+	−	−	−
Tetramethylthiuramdisulphide	−	20	−	−	−	−
"Titrol"	10%	5	−	−	−	−
Triethanolamine	1%	60	−	−	−	+

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Fig. 1.

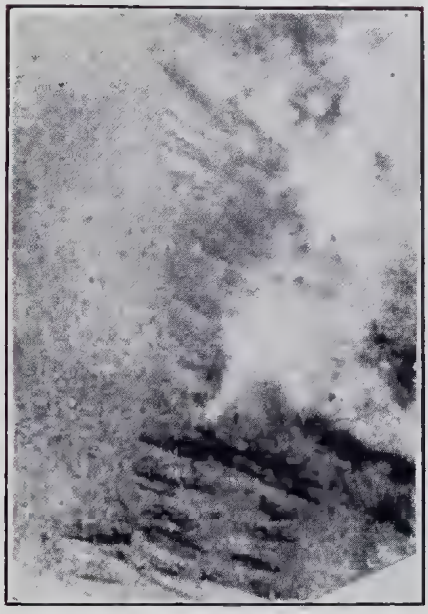

Fig. 2.

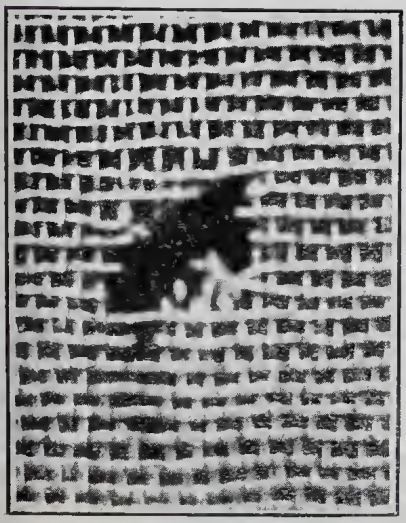

Fig. 3

Fig. 4.

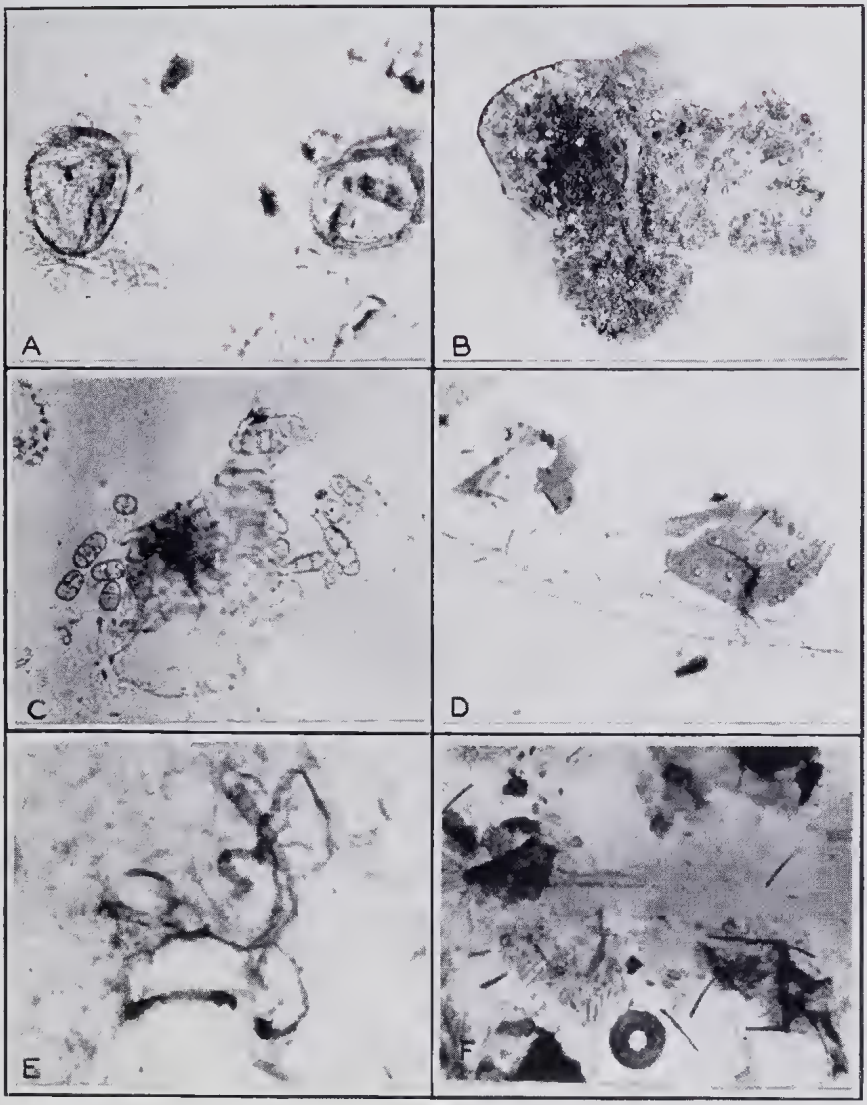

Fig. 1.

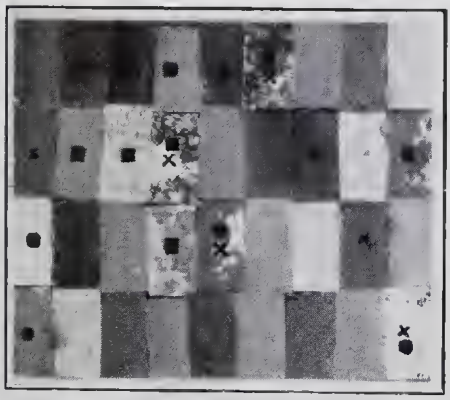

Fig. 2

	RED	DEXTRIN	DEXTRIN	STARCH	RED DEXTRIN			
RED	DEXTRIN	DEXTRIN	RED DEXTRIN			RED		STARCH
STARCH	RED		DEXTRIN	RED STARCH			RED	
STARCH								RED STARCH

Fig. 3.

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Explanation of Plates

Plate 1.

Fig. 1.—*Ctenolepisma longicaudata* Esch.

Fig. 2.—Damage on wallpaper × 138.

Fig. 3.—Damage on artificial silk net × 8.6.

Fig. 4.—Damage on artificial silk fabric. × 4.5.

Plate 2.

Fig. 1.—Fragments from contents of crops.

A. Pollen grains. × 276.
B. Edge of leaf. × 62.
C. Fungal spores. × 318.
D. Chitin showing bases of setae × 396.
E. Fibres from paper stained with Herzeberg's reagent. × 76.
F. Chitin and setae. × 310.

Fig. 2.—Section of wallpaper samples after test of one week.

Fig. 3.—Key to composition of samples shown in Fig. 2. The unlabelled samples contain the sizes, gum, glue and casein.